

Twenty-five years of vegetation change along a putative successional chronosequence on the Tanana River, Alaska¹

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Abstract: Along the Tanana River floodplain, several turning points have been suggested to characterize the changes in ecosystem structure and function that accompany plant community changes through primary succession. In the past, much of this research focused on a presumed chronosequence that uses space for time substitutions. Within this chronosequence, permanent vegetation plots repeatedly measured over time provide an excellent test of the turning points model. We analyzed both canopy and understory vegetation data collected since 1987 in the Bonanza Creek Experimental Forest at the Bonanza Creek Long Term Ecological Research site to address the following questions: (i) Do long-term changes in the densities of seedling, sapling, and mature trees and shrubs of the dominant woody taxa at each successional stage support the turning points model? (ii) How does the entire plant community change with time at each hypothesized turning point? (iii) Do we see evidence of directional and synchronous shifts in species composition across successional stages? We conclude that some aspects of vegetation change during the last 25 years were consistent with the turning points model; however, many changes were not consistent, indicating the potential roles of biological, environmental, landscape, and climate controls in vegetation patterns.

Résumé : Le long de la plaine inondable de la rivière Tanana, plusieurs moments décisifs ont été suggérés pour caractériser les changements de fonction et de structure de l'écosystème qui accompagnent les changements dans la communauté végétale tout au long de la succession primaire. Dans le passé, la plupart des travaux de recherche ont mis l'accent sur une chronoséquence présumée qui suit une approche synchronique. À l'intérieur de cette chronoséquence, des placettes échantillons permanentes de la végétation, mesurées à plusieurs reprises dans le temps, constituent un excellent test pour le modèle des moments décisifs. Nous avons analysé des données de végétation de la canopée et du sous-étage collectées depuis 1987 dans la forêt expérimentale de Bonanza Creek, à la station de recherche à long terme en écologie de Bonanza Creek, dans le but de s'attaquer aux questions suivantes : (i) Est-ce que les changements à long terme de densité des semis, des gaules et des arbres matures ainsi que des arbustes des taxons ligneux dominants à chaque stade de succession supportent le modèle des moments décisifs? (ii) De quelle façon la communauté végétale en entier change avec le temps à chaque moment décisif présumé? (iii) Voit-on des signes de changements directionnels et synchrones dans la composition en espèces à travers les stades de succession? Nous arrivons à la conclusion que certains aspects de la modification de la végétation au cours des derniers 25 ans ont été cohérents avec le modèle des moments décisifs. Cependant, plusieurs changements n'étaient pas cohérents, indiquant que des facteurs biologiques, environnementaux, paysagers et climatiques pourraient avoir un effet déterminant sur les patrons de végétation.

[Traduit par la Rédaction]

Introduction

The trajectory and rate of primary succession are influenced by interactions among stochastic events, community-level processes, and species life history traits (Billings 1938; Egler 1954; Connell and Slatyer 1977; Walker et al.

1986). Spatial variation and temporal changes in the environment, disturbance regime, and population sizes, combined with chance, contribute to the complexity of successional processes and outcomes across a landscape. Initially during primary succession, plant colonization depends on suitable microenvironmental conditions and seed disper-

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sal, which vary with landscape position and time (Walker and Chapin 1987; Fastie 1995). The influence of selective herbivory on plant competition also changes with spatial and temporal variation in herbivore population densities (Bryant and Chapin 1986; Kielland and Bryant 1998; Butler et al. 2007). The direct and indirect effects of flooding, fire, and insect/pathogen outbreaks further influence the course of primary succession (Foster et al. 1998; Ruess et al. 2009). Finally, species responses to changes in climate or environmental conditions, such as drought and permafrost thaw, may contribute to long-term changes in successional patterns (Johnstone et al. 2010).

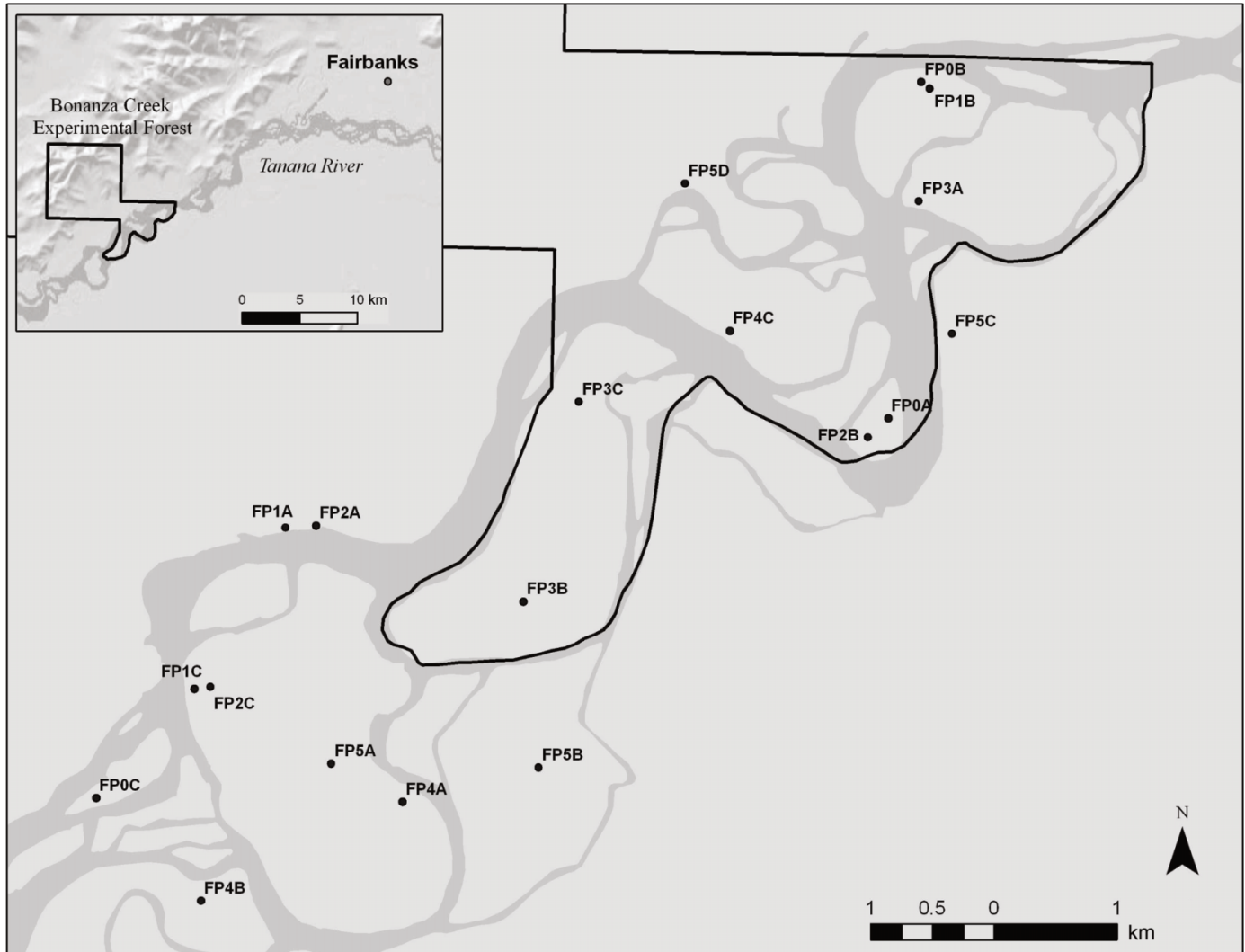
The number of potential successional trajectories along the Tanana River floodplain in interior Alaska is limited by species' life history traits, particularly those associated with seed dispersal, germination requirements, growth rate, flooding tolerance, shade tolerance, and life span (Kalliola et al. 1991). The low diversity of vascular plants in the boreal forest constrains the realm of successional possibilities and magnifies the importance of landscape-level recruitment and mortality events (Chapin et al. 2006). Characterization of the structure and physical properties of the dominant stand types on interior Alaskan floodplains (specifically the Chena and Tanana rivers) led to the hypothesis that one pathway represents the central tendency of succession on the Tanana River floodplain (Viereck 1970; Van Cleve et al. 1991; Viereck et al. 1993). These authors argued that this successional pathway progresses from willows (particularly *Salix alaxensis* (Andersson) Coville) to thinleaf alder (*Alnus incana* subsp. *tenuifolia* (Nutt.) Breit., hereafter *A. tenuifolia*) to balsam poplar (*Populus balsamifera* L.) to white spruce (*Picea glauca* (Moench) Voss) and finally to black spruce (*Picea mariana* (Mill.) BSP). However, early studies on Alaskan floodplains hypothesized that this sequence was one of many potential successional pathways (Drury 1956). For example, Drury hypothesized that the balsam poplar phase could be bypassed if there were rapid colonization by white spruce seedlings after initial vegetation establishment. He also hypothesized that it was possible that mixed white spruce stands could be relatively stable and may not transition to black spruce forests without flooding or underlying changes in site drainage.

The Bonanza Creek Long Term Ecological Research (BNZ LTER) program was designed to study primary succession of interior Alaskan floodplain forests by using a putative chronosequence of stands representing major transitions, or "turning points," in overstory composition during successional development (Van Cleve et al. 1991; Viereck et al. 1993; Yarie et al. 1998). Research sites were selected specifically to represent the six most important turning points: (i) initial stabilization of silt-bar alluvium by early plant colonists, (ii) formation of a complete vegetation canopy (willow) and surface organic layer, causing a shift in controls over nutrient cycling from primarily abiotic (e.g., drought, salinity) to biotic (e.g., litter quality), (iii) transition from willow to N-fixing alder dominance in the shrub canopy, causing rapid increases in ecosystem N accumulation (Van Cleve et al. 1971; Walker 1989; Uliassi and Ruess 2002), (iv) shift in dominance from shrubs (alder) to deciduous trees (balsam poplar), aided by the rapid growth of poplar when released from light limitation beneath the shrub

canopy, (v) replacement of balsam poplar by white spruce, facilitating the development of a continuous moss ground cover uninhibited by deciduous leaf litter, and (vi) development of permafrost resulting from the insulative properties of the moss cover, allowing black spruce to replace white spruce, which is less tolerant of the cold, poorly drained soils that occur with permafrost.

Recent studies have questioned the turning points model, particularly the hypothesized transition from white spruce to black spruce. Mann et al. (1995) proposed that the distributions of white and black spruce on the Tanana River floodplain are determined by site drainage, which is controlled principally by geomorphology rather than time since disturbance. They hypothesized that mature black spruce stands are restricted to poorly drained backswamps, while white spruce forests dominate the well-drained meander belt and are unlikely to succeed to black spruce in the absence of an additional disturbance, such as fire. Hollingsworth et al. (2006) found that occasional white spruce occurrence in black spruce stands was a function of site drainage and acidity and was not related to stand age, supporting the hypothesis that the distribution of black spruce on the Tanana floodplain is a function of underlying site drainage and fire history. These studies suggest that the substitution of time for space for the white spruce and black spruce stages of this chronosequence may have been based on false assumptions, as has been shown for chronosequence studies in other ecosystems (Fastie 1995; Johnson and Miyanishi 2008), and that the long-term monitoring of vegetation could clarify the actual pattern of successional change with time.

Here, we analyze a long-term data set (20 years) on vascular and nonvascular plant species from the BNZ LTER chronosequence to test whether changes in stand structure and composition support the turning points model of primary succession. Specifically, we addressed the following research questions: (i) Do long-term changes in the densities of seedling, sapling, and mature trees and shrubs of the dominant woody taxa at each successional stage support the turning points model? We would expect (a) early-colonizing woody species (primarily willows) to decline rapidly by midsuccession, (b) seedlings and saplings of midsuccessional woody species (thinleaf alder and balsam poplar) to reach maximum abundance prior to midsuccession and mature alder and poplar to reach maximum abundance in midsuccession, and (c) late-successional woody species (white and black spruce) to appear as seedlings and saplings in early or midsuccession and peak as mature trees by late succession. (ii) How does the entire plant community change with time at each hypothesized turning point? The turning points model predicted increases in moss abundances at the poplar – white spruce transition and a further increase in mosses with the development of permafrost but said little about changes in the understory plant community. (iii) Do we see evidence of directional and synchronous shifts in species composition across successional stages? These directional shifts could be related to regional fluctuations in herbivore populations (Butler et al. 2007) or recent changes in climate that have influenced soil moisture, permafrost, river hydrology, and disturbance regimes (Chapin et al. 2010).

Fig. 1. Map of Bonanza Creek Experimental Forest and the BNZ LTER long-term floodplain vegetation monitoring sites.

Materials and methods

Study site and site selection

Bonanza Creek Experimental Forest, one of two primary research areas for the BNZ LTER, encompasses roughly 5000 ha approximately 30 km southwest of Fairbanks, Alaska, and includes a section of the Tanana River floodplain (Fig. 1). LTER research at the Bonanza Creek Experimental Forest focuses on the processes and patterns associated with succession following disturbance in the uplands and floodplains.

BNZ LTER was initiated to monitor and study the turning points described by Viereck et al. (1993). Therefore, sites were selected specifically to represent a chronosequence of primary successional forest development with an emphasis on the six turning points described above (Van Cleve et al. 1991). It was proposed that if this chronosequence of sites were monitored over the long term, it would be possible to observe the successive transitioning of one forest type into another. Thus, over time, early-successional sites (newly vegetated alluvium) would become more similar to midsuccessional sites (alder thickets and balsam poplar stands) and

midsuccessional sites would become more similar to late-successional sites (white and black spruce stands). Permanent vegetation plots were established on the floodplain in 1987 with some early-succession sites reestablished between 1993 and 1995. Three or four replicates sites separated by up to several kilometres were established in each of the six hypothesized turning points and these replicates represent a stage of succession assuming that the stages were a chronosequence (Table 1). Because BNZ LTER monitoring was established in stands hypothesized to be turning points, these stands likely represent a relatively small proportion of the floodplain landscape, which is comprised more by stands representing more stable stages of vegetation. The exception to this would be the late-successional white and black spruce sites that are fairly common on the landscape.

Study sites at BNZ LTER are named according to the following scheme: habitat (FP = floodplain), successional stage (0–5), and replicate (A–D) (Table 1). At the time of establishment, FP0 represented early colonization of bare alluvium, FP1 represented the shift from open willow to a dense closed thinleaf alder thicket, FP2 sites encompassed the turning point from an open poplar stand with a dense al-

Table 1. Description of successional stages and turning points including names of study sites and a description of the vegetation at first measurement and again in 1997.

Turning point	Study sites	Mineral soil pH (range)	Soil drainage class	Tree age (range in years)	Terrace height (m) taken from LIDAR and averaged across each site (range)	Successional stage and vegetation in 1984	Successional stage and vegetation in 1997
0. Shift from bare silt bar to initial plant colonization	FP0A, FP0B, FP0C	7.31–7.97	Moderately well drained	0–5	1.2–1.7	Stage 0: river or ephemeral sandbar, no vegetation (vegetation first measured in 1995 (FP0A) and 1996 (FP0B and FP0C))	Stage I to 0: willow colonization, buried by fluvial deposition in 1997, resetting vegetation to near stage 0
1. Shift from open willow to closed shrub community	FP1A, FP1B, FP1C	7.3–7.9	Somewhat poorly drained	0–20	1.7	Stages II and III: open willow	Stages III and IV: open to closed shrub
2. Shift in dominance from shrubs to trees	FP2A, FP2B, FP2C	7.4–8.1	Moderately well drained	40–60	2.3	Stage IV: closed shrub with young balsam poplar	Stages V and VI: young balsam poplar with alder understory
3. Shift in dominance from deciduous to coniferous trees and establishment of feather-moss	FP3A, FP3B, FP3C	7.18–7.94	Somewhat poorly drained	50–100	2.4–3.1	Stage VII: balsam poplar with young white spruce	Stage VII: balsam poplar with young white spruce
4. Development of permafrost	FP4A, FP4B, FP4C	5.42–8.03	Somewhat poorly drained	150–200	2.9	Stage VIII: mature floodplain white spruce	Stage VIII: mature floodplain white spruce, stem density reduced by snow breakage in 1991 followed by insect mortality
5. Mature black spruce	FP5A, FP5B, FP5C, FP5D	6.08–7.88	Somewhat poorly drained	150–200	2.8–3.6	Stage XI: open black spruce (FP5A, FP5C, and FP5D), open white spruce with black spruce seedlings/saplings (FP5B)	Stage XI: open black spruce (FP5A, FP5C, and FP5D), open white spruce with black spruce seedlings/saplings (FP5B)

der understory to closed balsam poplar canopy, FP3 sites were placed at the transition from balsam poplar dominance to white spruce dominance, FP4 sites were mature white spruce stands with a thick organic horizon and well-developed shrub layer, and FP5 sites were late-successional evergreen stands. These were further subdivided into (a) mixed black spruce – white spruce with little or no permafrost and (b) black spruce dominated sites with permafrost (Van Cleve et al. 1991; Viereck et al. 1993). Additional evidence supports the differences in surface age and associated biochemical properties of these stands (Table 1): pH decreased and terrace height (analogous to surface age) and tree age increased across the chronosequence of sites.

Vegetation sampling

One permanent 50 m × 60 m plot containing twenty 1 m² vegetation plots was established at each site. Sites at early turning points (FP0, FP1, and FP2) were remeasured every 1–2 years, while those in older stages (FP3, FP4, and FP5) were remeasured every 4–5 years. Visual estimates of percent cover were made for forbs, lichens, shrubs, trees, fungi, surface mineral soil, disturbed organic soil, fine woody debris, coarse woody debris, litter, standing dead, and water; however, anything above 1 m in height was not considered in these percentage estimates. Values from 1% to 10% and from 90% to 100% are reported in unit increments, from 10% to 90% in increments of 5, and less than 1% as T for trace.

Seedlings, saplings, and tall shrubs were tallied at each site. Prior to 2006, all seedlings, saplings, and tall shrubs were counted within twenty 4 m² circular plots centered on one corner of the 1 m² vegetation plots. This method was discontinued in 2006 to better quantify the presence of clumped shrub species. Beginning in 2006, all seedlings, saplings, and tall shrubs were counted in a 2 m wide transect along one 50 m and one 60 m boundary of the control plot. Tallies noted each individual and delineated them into 1 cm basal diameter size class. Tree seedlings were less than 1.37 m in height and saplings were greater than 1.37 m in height with a diameter less than 2.5 cm measured at breast height (1.37 m). All shrubs greater than 1 m tall were counted. Tree density was measured for each canopy species at each site and methods are described in detail in McGuire et al. (2010). Here, we report tree densities over time for balsam poplar and white spruce across all successional stages that they occur in. Raw data files are available at www.lter.uaf.edu/data_detail.cfm?datafile_pkey=174 and www.lter.uaf.edu/data_detail.cfm?datafile_pkey=175.

Data analysis

Tall shrub and seedling/sapling densities

Changes in density of woody plants were analyzed using repeated-measures ANOVA. Normality of density values was assessed using a Kolmogorov–Smirnov test. Density deviated from normality for a handful of species, but the deviations were slight and could not be corrected with transformation; since ANOVA tends to be robust to small deviations from normality, we proceeded with the analysis on untransformed data. We used Mauchly's test of sphericity to assess the assumption of homogeneity of variance. Where

data violated the assumption, we use values following the Huynh–Feldt correction. When the effect of site was significant, differences in density among pairs of sites were assessed using Tukey's honestly significant difference post hoc test. All statistical analyses were conducted in SPSS version 16.0.1.

Species richness and composition

Changes in species richness among successional stages (FP0s through FP5s) were evaluated using linear regression of species richness on year. The assumption that species richness is normally distributed was confirmed for all stages using the Kolmogorov–Smirnov test (all $P > 0.05$).

Shifts in functional groups across successional stages were analyzed using data from the last year of measurement with one-way ANOVAs as a proportion of total percent cover for each plant functional group (deciduous shrubs, deciduous trees, evergreen shrubs, evergreen trees, forbs, graminoids, lichens, mosses, *Sphagnum*, and nonvegetation including litter, surface mineral, and water). Tukey–Kramer post hoc tests were used to distinguish significance between groups.

Based on cover data, community compositional changes among sites within successional stages and among stages were analyzed through nonmetric multidimensional scaling (NMDS) ordination analysis (PC-ORD version 4.25). NMDS is an ordination technique well suited for ecological community data, which tend to be nonnormal or occurring along arbitrary or discontinuous scales. Sorensen distance measures, with random starting configurations, with 10 runs of real data and 20 runs of randomized data were used, the latter to provide the basis for a Monte Carlo test of significance for each dimension or axis. Dimensionality was assessed by comparing the final stress values among the best solutions and selecting the lowest dimensionality that meets the criterion of maximum stress. We present the two dimensions in our figure with accepted maximum stress.

To examine our hypotheses concerning the coincidence of understory dynamics with overstory turning point transitions, we looked at differences in species composition among measurement years (1980s, 1990s, or 2000s) and successional stages (three or four replicate sites) using the nonparametric randomization procedure multiresponse permutation procedure (MRPP). MRPP tests for differences among a priori groups (Clarke 1993). We were interested in (i) similarity among replicate sites at a given successional stage for each measurement year and, more specifically, (ii) whether there was a significant tendency for successional stages to transition towards the beginning of the next successional stage. For example, was there a significant difference in species composition between the FP0s and FP1s in the 1980s, and over the next two decades, did the FP0s transition to where FP1s were in the 1980s? With MRPP, we used within-group homogeneity or effect size (A) to examine how similar a given successional stage in the 1980s, 1990s, and the 2000s was to the successive stage in the 1980s. The A statistic is analogous to a similarity index with a maximum value of 1 if all samples within a group are identical. In this way, we could examine whether or not sites in a given successional stage have become more similar to the next successional stage over time.

Table 2. Stem density (stems·ha⁻¹, mean ± SE) of the most abundant woody species at each stage of succession.

Species	Decade	FP0	FP1	FP2	FP3	FP4	FP5
(a) Early-successional species							
<i>Salix alaxensis</i>	1980s	625±318	12416±7169	250±306	—	—	—
	1990s	500±265	6958±5043	208±255	—	—	—
	2000s	2096±1980	28±34	28±34	—	—	—
<i>Salix interior</i>	1980s	160000±145010	30750±22719	—	—	—	—
	1990s	47083±11761	9500±7453	—	—	—	—
	2000s	41528±8509	1333±1632	—	—	—	—
<i>Salix lasian-dra</i>	1980s	—	3250±2039	42±51	—	—	—
	1990s	125±153	1666±1350	—	—	—	—
	2000s	—	28±34	33±42	—	—	—
(b) Midsuccessional species							
<i>Alnus tenui-folia</i>	1980s	—	583±368	4292±2886	3875±1846	2167±2654	—
	1990s	—	14041±665	7792±2614	7167±3224	2875±3294	—
	2000s	7764±8364	5544±5243	4867±3004	3666±2299	1994±2443	—
(c) Late-successional species							
<i>Alnus viridus</i>	1980s	—	—	—	—	875±1072	2250±2598
	1990s	—	—	—	—	666±669	1750±2021
	2000s	—	—	—	—	2533±1618	1750±2021
<i>Betula neoa-laskana</i>	1980s	—	41±51	—	—	1875±1215	812±567
	1990s	—	125±153	—	—	1708±969	344±397
	2000s	55±34	—	—	—	928±806	363±147
<i>Salix arbus-culoides</i>	1980s	—	167±204	—	—	—	625±552
	1990s	—	—	—	—	—	2500±1826
	2000s	—	—	—	—	—	172±163
<i>Salix glauca</i>	1980s	—	—	—	—	—	2844±1095
	1990s	—	—	—	—	—	1688±822
	2000s	—	—	—	—	—	1438±744
<i>Salix pulchra</i>	1980s	—	—	—	—	—	3781±2571
	1990s	—	—	—	—	—	2063±1904
	2000s	—	—	—	—	33±41	367±159

Note: Stem density of the dominant tree species at each successional stage is shown in Fig. 2. Species were classified into successional stages (early, mid-, and late) based on a one-way ANOVA of differences among sites (see Materials and methods: Data analysis). The site with highest abundance of each species during each decade of measurement is indicated by bold type. A dash indicates that a species was absent from a site. Significance tests of differences among sites and years are summarized in Table 3.

Finally, we used indicator species analysis (Dufrene and Legendre 1997) to characterize the species that define a successional stage at a given measurement time. Indicator species analysis produced indicator values for each species within a given successional stage based on *faithfulness* (presence within a stage) and *exclusiveness* (absence from other stages). Indicator values were then tested for statistical significance using a Monte Carlo technique (McCune and Grace 2002). We performed an indicator species analysis for successional stages in the 1980s and then again in the 2000s. In this way, we could assess more specifically which species were changing over time.

Directional changes in functional group percent cover over time

Based on the NMDS ordination, we identified distinct suc-

cessional stages that exhibited the least variation in under-story species composition among years (FP4s and FP5s). Because these sites do not appear to be undergoing rapid successional transitions, we were interested in consistent directional changes in functional group composition among stage replicates (i.e., sites). For each site within these two late-successional stages, we conducted matched paired *t* tests to determine whether the proportion of the total vegetation cover for each functional group changed between the last year and first year of data collection at that site. Significant changes in functional group cover that occurred in every site within each stage were further explored by plotting data from an intermediate year to verify the directionality of changes. We used data from the decades of 1980, 1990, and 2000 for the FP4 sites but were limited to shorter intervals for the FP5 sites with data from the early 1990s, early 2000s, and late 2000s.

Table 3. Results of repeated-measures ANOVA on stem density of woody plant species.

Species	Year			Year × site			Site		
	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>
(a) Early-successional species									
<i>Populus balsamifera</i>	0.345	1.476	0.648	10.376	7.38	<0.001	8.714	5	0.001
<i>Salix alaxensis</i>	3.207	1.898	0.060	4.096	9.489	0.002	4.074	5	0.019
<i>Salix interior</i>	1.753	1.439	0.204	1.102	7.195	0.402	3.691	5	0.027
<i>Salix lasiocarpa</i>	2.976	2	0.069	2.866	10	0.015	4.353	5	0.015
(b) Midsuccessional species									
<i>Alnus tenuifolia</i>	2.027	2	0.152	1.762	10	0.119	3.105	5	0.046
<i>Picea glauca</i>	1.593	2	0.223	1.262	10	0.301	2.288	5	0.107
(c) Late-successional species									
<i>Alnus viridus</i>	4.491	2	0.021	2.110	10	0.062	0.755	5	0.597
<i>Betula neoalaskana</i>	1.287	2	0.293	0.799	10	0.631	3.590	5	0.029
<i>Picea mariana</i>	0.414	2	0.665	0.477	10	0.890	1.286	5	0.328
<i>Salix arbusculoides</i>	2.135	1.733	0.148	2.275	8.666	0.060	3.204	5	0.046
<i>Salix glauca</i>	1.089	1.533	0.340	1.318	7.666	0.251	6.571	5	0.003
<i>Salix pulchra</i>	0.498	1.781	0.593	0.617	8.907	0.769	7.274	5	0.002

Note: Significant results are highlighted in bold. The degrees of freedom are adjusted (using the Huyn–Feldt correction) in some cases for data that violated the assumption of sphericity in the covariance matrix.

Fig. 2. Stem density (log scale) of balsam poplar (*Populus balsamifera*) (a) seedlings and saplings and (b) canopy trees at six floodplain successional stages over 25 years. Values are means ± 1 SE (*n* = 3 plots per site except at FP5 where *n* = 4 plots).

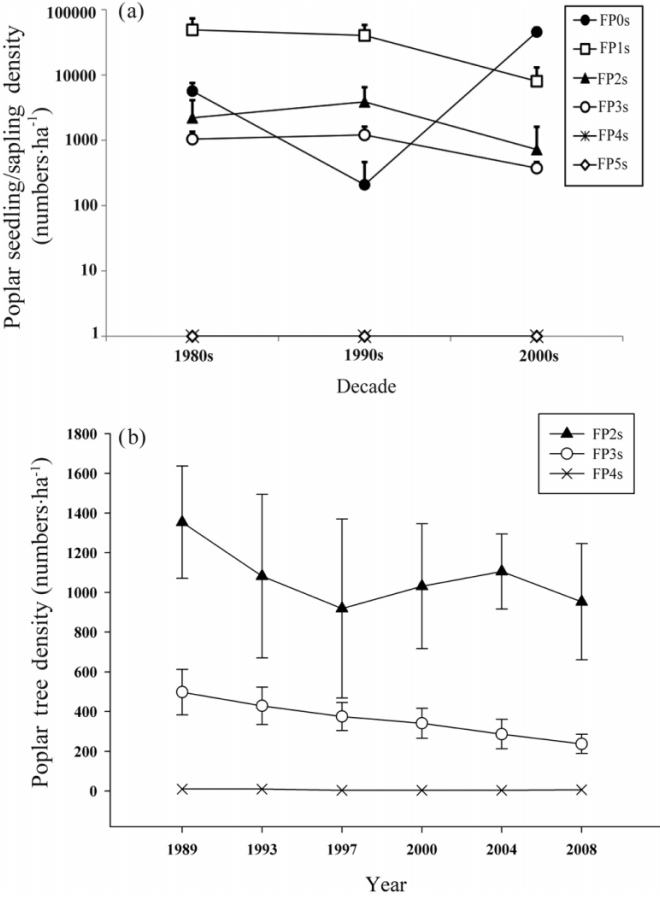


Fig. 3. Stem density (log scale) of white spruce (*Picea glauca*) (a) seedlings and saplings and (b) canopy trees at six floodplain successional stages over 25 years. Values are means ± 1 SE (*n* = 3 plots per site except at FP5 where *n* = 4 plots).

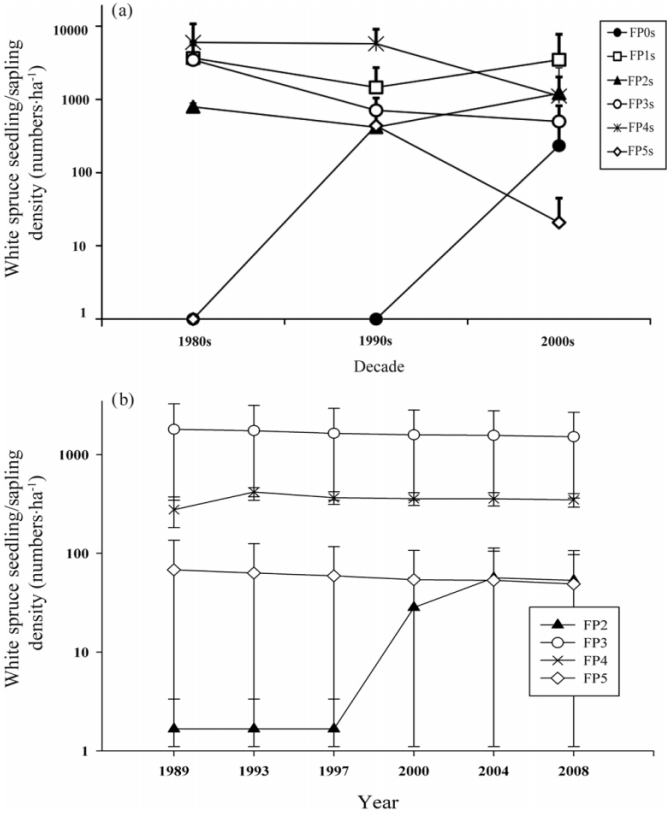


Table 4. Trends in species richness over time at six floodplain sites.

Site	Slope	Significance test
FP0	0.927	$t = 6.561$, $df = 1$, $P < 0.0005$
FP1	0.153	$t = 0.409$, $df = 1$, $P = 0.695$
FP2	0.294	$t = 0.813$, $df = 1$, $P = 0.443$
FP3	-0.338	$t = 0.951$, $df = 1$, $P = 0.373$
FP4	-0.361	$t = 1.025$, $df = 1$, $P = 0.340$
FP5	0.257	$t = 0.839$, $df = 1$, $P = 0.421$

Note: The slope is reported here as the standardized regression coefficient (β) and is determined by a regression of vascular plant species richness on time. The significance of each slope is tested using a Student t test with the null hypothesis that $\beta = 0$. The significant slope ($P < 0.05$) is highlighted in bold.

Results

Changes in tall shrub and tree species densities across all sites

Density (and basal area, data not shown) of early-successional species changed through time as predicted by the successional chronosequence. Density of *S. alaxensis* also increased at the youngest sites (FP0s) and declined at FP1 and FP2 sites over time. Its density at FP0s in the 2000s, however, was substantially less than its density at FP1s in the 1980s, suggesting that the actual pattern of change has deviated somewhat from the predicted pattern. *Salix interior* Rowlee, the dominant species on uncolonized sandbars, declined through time at FP0s; however, changes in the density of *Salix lasiandra* Benth., in contrast, did not conform to expectations (Tables 2a and 3). This species reached maximum dominance in the 1980s and, despite a small amount of colonization in the 1990s, was absent from FP0s (and nearly absent from FP1s and FP2s) by the most recent sampling interval. Balsam poplar seedling/sapling density increased significantly through time at the youngest sites (FP0s), declined significantly over time at FP1 sites, and was largely absent from the understory of later successional sites (Fig. 2a). In the 1980s, the FP2s had approximately the same number of balsam poplar saplings and trees and both declined over the next 20 years (Fig. 2). Finally, balsam poplar tree density decreased in the FP3s over time, was nearly absent in the FP4s, and did not occur in the FP5s.

Changes in the density of thinleaf alder, an early- and midsuccessional dominant (which reached maximum abundance at the FP2 sites in the 1980s), were consistent with expectations, becoming more abundant at the younger sites through time (Tables 2b and 3). The rapid recruitment of thinleaf alder at the youngest sites (FP0s) in the most recent sampling interval is notable, given the failure of some early-successional species (e.g., *S. lasiandra* and *S. alaxensis*) to establish successfully at those sites. There were an order of magnitude more seedlings of thinleaf alder in the FP0 sites in 2000 than at the FP1 sites in the 1980s. Moreover, thinleaf alder remained abundant at the later successional (FP3s and FP4s) sites throughout the time period of this study. At all sites, however, it reached a peak of abundance in the 1990s.

The density of white spruce did not change as predicted (Fig. 3). We expected white spruce seedling/sapling density

to increase in the younger sites (particularly FP2s and FP3s) and decline in FP4s. Although none of the changes in white spruce density were statistically significant (Table 3), white spruce seedling and sapling density declined substantially (from 6000 to 1111 stems·ha⁻¹) at the white spruce sites (FP4s). By the most recent sampling period, white spruce seedlings were substantially less abundant across these floodplain sites (Fig. 3a). As expected, there was a gradual transition of saplings to trees in the FP2s over time (Fig. 3); however, the density of white spruce in the FP2s in 2008 was an order of magnitude less than in the FP3s and FP4s at our first sampling date (1980s).

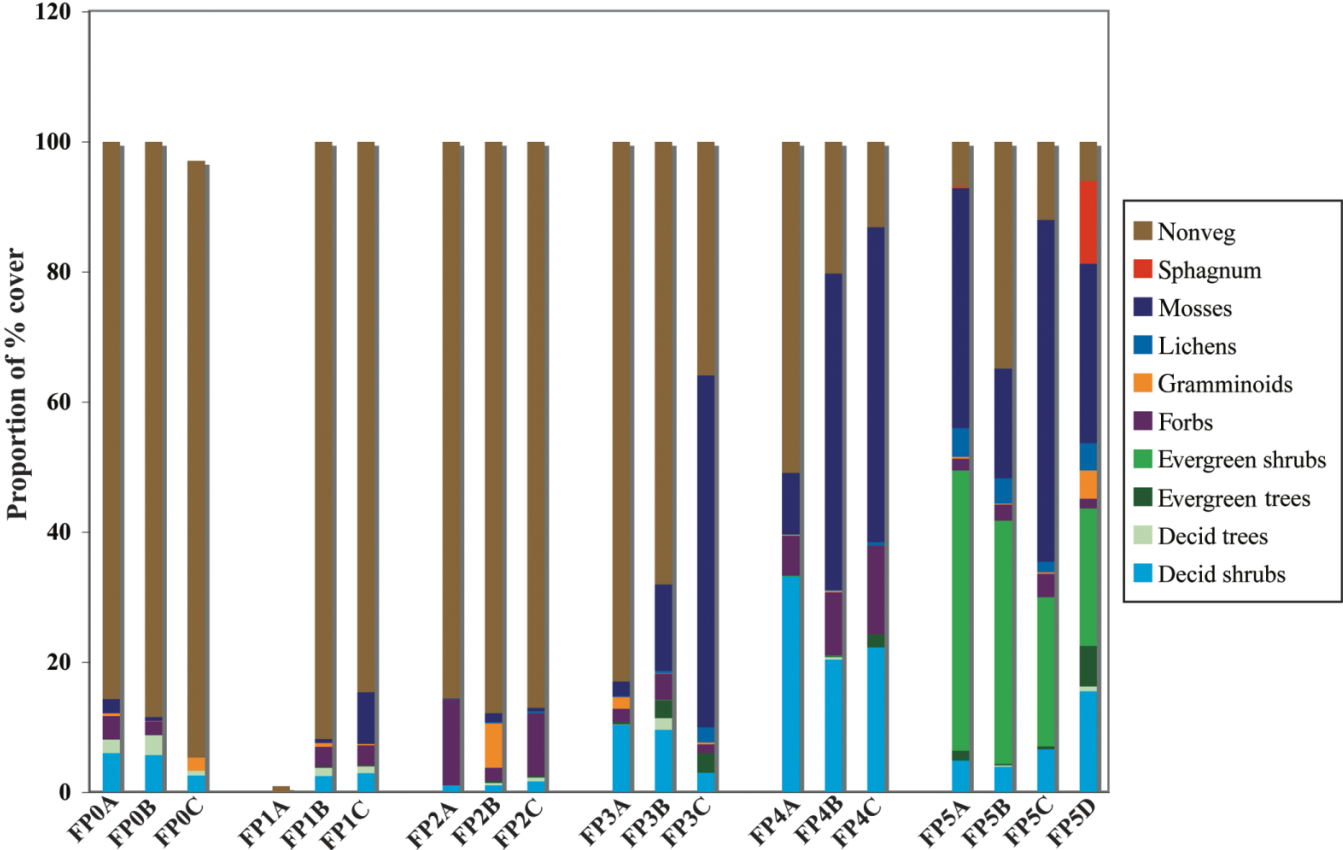
Late-successional understory woody species also failed to change as predicted by the successional chronosequence. Black spruce density did not change significantly across time and there was no recruitment of black spruce in any site other than the FP5 sites, suggesting that the observed decline in white spruce abundance at the FP4 sites was not a consequence of the predicted replacement of by black spruce (Table 3). A similar pattern was observed for three other late-successional species: *Salix arbusculoides* Anderss., *Salix glauca* L., and *Salix pulchra* Cham. The density of all three species declined over time within the FP5 sites, but none of these species successfully established in other sites (Tables 2c and 3). Only one late-successional species, alder (*Alnus viridis* subsp. *fruticosa* (Rupr.) Nym.), conformed somewhat with expectations. This species increased in density at the FP4 sites and became less abundant at the FP5 sites (where it reached maximum abundance in the 1980s); however, alder was completely absent from the FP3 sites, suggesting that its recruitment may not be due to primary successional processes.

Changes in species richness and composition

Species richness increased significantly over time at the youngest sites (FP0s) (Table 4), from an average of 10.3 ± 0.6 (mean \pm SE, $n = 3$ plots) species per plot in the 1980s to 21.6 ± 1.0 species per plot in 2008. This increase in species richness brought these sites within the range of values for species richness documented at older sites. Despite fluctuations through time at individual sites, the overall number of species (vascular and nonvascular) per plot, averaged across all stages, remained unchanged over the 30 years of sampling (32 ± 2.6 in the 1980s and 32 ± 2.8 in the 2000s).

We examined the shifts in functional groups (i.e., plant growth forms and nonvegetation) at the last measurement (2008) for each site (Fig. 4) and looked for significant shifts in functional types between successional stages. Data show significant differences in the proportion of deciduous shrubs ($F = 13.279$, $df = 5$, $P < 0.0001$), deciduous trees ($F = 3.532$, $df = 5$, $P = 0.031$), evergreen trees ($F = 22.897$, $df = 5$, $P < 0.0001$), forbs ($F = 4.521$, $df = 5$, $P = 0.013$), lichens ($F = 11.883$, $df = 5$, $P < 0.0001$), mosses ($F = 3.537$, $df = 5$, $P = 0.031$), and nonvegetation ($F = 18.355$, $df = 5$, $P < 0.0001$) across successional stages. Tukey-Kramer post hoc tests revealed that deciduous shrubs are significantly more abundant in the FP4s, deciduous trees make up a decreasing proportion of plant cover as successional age increases, evergreen trees and lichens are significantly greater in the FP5s, and forbs are significantly greater in the FP0s and FP5s.

Fig. 4. Proportion of percent cover for growth forms of the understory (less than 1 m height) at each site for the last measurement (2000s).



Across all years, there was substantial variability in species composition among replicate sites in early-successional stages (FP0s, FP1s, and FP2s), particularly among the FP2 stands. This is shown by the area of the ellipse that each successional stage (across measurement years) occupies in the ordination space (Fig. 5). There is a distinct break in species composition between early- and mid-successional stages (FP0s, FP1s, and FP2s) and mid- and late-successional stages (FP3s, FP4s, and FP5s), indicating a large shift in species composition. Based on species compositional shifts over time, the FP3s appear to be converging towards the FP4s; however, there is also some overlap between the FP5s and FP3s. In other words, understory species are beginning to appear in the FP3s that persist in both the FP4s and FP5s. Late-successional sites (FP4s and FP5s) show very little variation in species composition among replicate stands or over time compared with the early-successional sites, as demonstrated by the tightness of replicate site groupings. Interestingly, there is also no overlap between the FP4s and FP5s (Fig. 5).

MRPP results show that over time, the FP0s are becoming more similar to what the FP1s were like in the 1980s. In fact, there is no significant difference between the FP0s in the 2000s and the FP1s in the 1980s (Fig. 6). The FP1s are consistently and repeatedly significantly different in species composition from the FP2s ($P < 0.05$), as are the FP2s from the FP3s ($P < 0.05$) and the FP3s from the FP4s ($P < 0.05$) (Fig. 6). There is no apparent convergence of the FP4s to the FP5s, and the FP4s were significantly different from the

FP5s in the 1980s ($P < 0.01$). Indicator species analysis revealed species specific to each successional stage (Table 5). Three species that were indicator species for the FP1s in the 1980s are currently indicator species for the FP0s. These species are *Equisetum variegatum* Schleich. ex F. Weber & D.M.H. Mohr, balsam poplar, and *S. interior*. These results are consistent with our MRPP results, which show a shift in species composition as predicted by successional theory in the early-successional sites. However, no other current successional stage shared indicator species with past successional stages. Mid-successional sites (FP2s and FP3s) had few indicator species. In the 1980s, the only indicator species for the FP2s was thinleaf alder, and during the 2000s, the only indicator species was the forb *Moehringia laterifolia* (L.) Fenzl (Table 5). This suggests that these young mid-successional sites share many species with other sites along the chronosequence and therefore may define transitions between communities and that these sites are more defined by structure of the vegetation rather than composition. This could explain some of the variability in overall species composition among the FP2 and FP3 sites revealed in the NMDS analysis (Fig. 5). Late-successional sites (FP4s and FP5s) have the highest number of indicator species, and the FP5s (black spruce dominated stands) in particular show a large consistency in indicator species over the last 25 years (Table 5). Black spruce stands also show the highest functional diversity with graminoids, forbs, deciduous shrubs, evergreen shrubs, evergreen trees, mosses, and lichens represented. These understory plant community results indicate

Fig. 5. NMDS ordination of floodplain successional chronosequence sites. Each successional stage is replicated three (or four) times and across three measurement intervals. Ellipses are drawn around each successional stage for each of interpretation. The arrow represents the classic linear successional paradigm, as depicted by the turning points model, excluding the black spruce (*Picea mariana*) (FP5) sites.

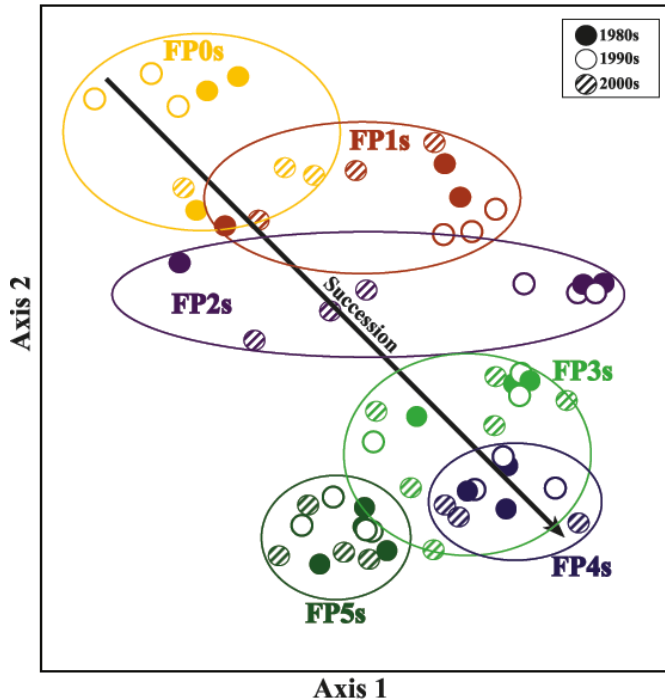
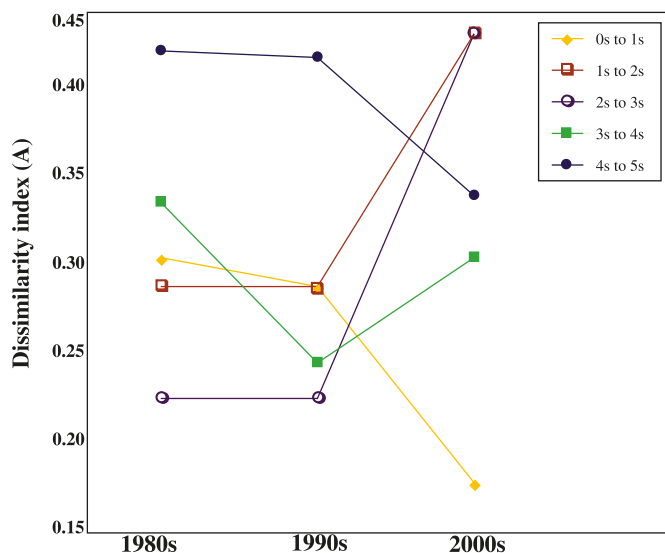


Fig. 6. Changes in effect size (A) from MRPP analysis of the floodplain successional chronosequence. Effect size represents a dissimilarity index where higher A values are more dissimilar. Each current (2000s) successional stage ($n = 3$ or 4 depending on the number of sites) was compared with the next successional stage in the 1980s, 1990s, and 2000s. All stages are significantly different in species composition from the next successional stage, except for the FP0s in the 2000s and the initial FP1s in the 1980s where $A = 0.17$.



that if white spruce stands do eventually shift to black spruce dominated stands, the time scale involved is extremely long and therefore undetectable in 25 years of study.

Directional and synchronous shifts in species composition across time

The FP4s and FP5s (white and black spruce stands) did not appear to be undergoing rapid successional transitions: there was minimal variation in understory species composition across years and a distinct separation between the two successional stages. These stages were therefore examined for directional changes in functional group composition that could be attributed to nonsuccessional controls. A significant decline in the proportion of total vegetation cover comprised of forbs was found in each FP4 and FP5 site between the 1980s (for FP4s) – 1990s (for FP5s) and the 2000s (both FP4s and FP5s) ($P < 0.003$) (Fig. 7). No consistent directional changes were found for any other functional group; however, the proportion of moss cover (excluding *Sphagnum*) significantly increased at FP4B, FP4C, and FP5C, while the proportion of *Sphagnum* cover significantly increased at FP5D ($P < 0.01$).

Discussion

The turning points model describing a primary successional sequence was developed based on landscape- and stand-level observations of the differences in dominant species and soil characteristics across various Alaskan floodplains (Drury 1956; Viereck 1970). To test this generalization of succession, specific sites were established and monitored to study long-term changes in plant community composition across a chronosequence. We found some evidence of long-term vegetation change that supports the turning points model, but we also found trajectories of change that suggest significant deviations from this model. These deviations have important implications for our understanding of community and ecosystem dynamics, particularly with respect to the predictability of successional change in interior Alaska (Kurkowski et al. 2008; Johnstone et al. 2010). Deviations from the expected pathway of succession may also indicate a more important influence of climate, landscape features, and disturbance agents, such as vertebrate herbivores and fire, than previously described.

Observed patterns consistent with the turning points model

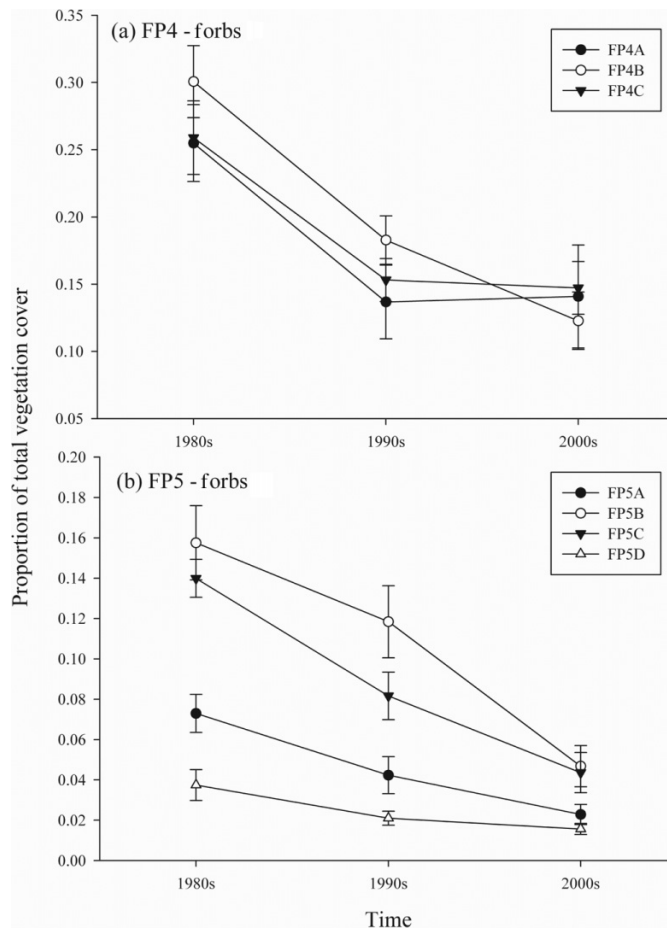
Some of the observed long-term changes in plant composition were predicted and described by the turning points model (Viereck et al. 1993). For example, we found that the current FP0 sites were not significantly different in species composition from the FP1 sites 20 years ago, demonstrating that the closed willow–alder thickets developed from open willow–silt bar sites. The success of *S. interior* and *Equisetum* spp. at colonizing the earliest successional sites (FP0s currently and the FP1s in the past), combined with the rapid density increases of balsam poplar seedlings/saplings and *S. alaxensis* from the 1990s through the 2000s at the FP0 sites, is consistent with their life history strategies and concurs with previous studies on the Tanana River floodplain (Viereck et al. 1993; Walker et al. 1986). As ex-

Table 5. Indicator species determined by species indicator analysis for each successional stage in the 1980s and again in the 2000s.

FP0s	FP1s	FP2s	FP3s	FP4s	FP5s
<i>Calamagrostis</i> sp. (G), 2000s	<i>Carex aurea</i> (G), 2000s	<i>Moehringia laterifolia</i> (F), 2000s	<i>Bryum</i> sp. (M), 1980s	<i>Goodyera repens</i> (F), 1980s	<i>Arctogrostis latifolia</i> (G), 1980s
<i>Hordeum jubatum</i> (G), 2000s	<i>Equisetum variegatum</i> (F), 1980s	<i>Alnus tenuifolia</i> (DS), 1980s	<i>Peltigera rufescens</i> (L), 1980s	<i>Cornus canadensis</i> (F), 2000s	<i>Carex bigelowii</i> (G), 2000s
<i>Juncus alpinus</i> (G), 1980s	<i>Leptarrhena pyrolifolia</i> (F), 1980s		<i>Peltigera canina</i> (L), both	<i>Geocaulon lividum</i> (F), 2000s	<i>Equisetum scipoides</i> (F), 2000s
<i>Castilleja caudata</i> (F), 2000s	<i>Salix interior</i> (DS), 1980s			<i>Monesis uniflora</i> (F), 2000s	<i>Stelleria longipes</i> (F), both
<i>Equisetum variegatum</i> (F), 2000s	<i>Salix pseudomyrsinites</i> (DS), 1980s			<i>Pyrola grandiflora</i> (F), 2000s	<i>Rubus chaemorus</i> (DS), 2000s
<i>Hedysarum boreale</i> (F), 2000s	<i>Salix hasata</i> (DS), 2000s			<i>Mertensia paniculata</i> (F), both	<i>Arctostaphylos rubra</i> (DS), both
<i>Salix interior</i> (DS), 2000s	<i>Populus balsamifera</i> (DT), 1980s			<i>Ribes trifolium</i> (DS), 2000s	<i>Salix pulchra</i> (DS), both
<i>Populus balsamifera</i> (DT), 2000s				<i>Rosa acicularis</i> (DS), 2000s	<i>Ledum groelandicum</i> (ES), 2000s
				<i>Rubus arcticus</i> (DS), 2000s	<i>Empetrum nigrum</i> (ES), both
				<i>Viburnum edule</i> (DS), both	<i>Vaccinium uliginosum</i> (ES), both
				<i>Linnaea borealis</i> (ES), both	<i>Vaccinium vitis-idaea</i> (ES), both
				<i>Eurhynchium pulchellum</i> (M), 1980s	<i>Picea mariana</i> (ET), both
				<i>Hylocomium splendens</i> (M), 1980s	<i>Aulocomium palustre</i> (M), both
				<i>Polytrichum juniperum</i> (M), 2000s	<i>Dicranum</i> sp. (M), 2000s
				<i>Ptilium crista-candensis</i> (M), 2000s	<i>Pleurozium schreberi</i> (M), 1980s
					<i>Cladina rangerfina</i> (L), both
					<i>Cladonia</i> spp. (L), both
					<i>Peltigera leucophlebia</i> (L), both
					<i>Peltigera scabrosa</i> (L), 2000s

Note: The FP0s began measurement in the 1990s, so no 1980 indicator species are shown. Each stage is made up of three sites and indicator species represent species that are present across all three sites and absent from other successional stages. Species are grouped by functional group: G, graminoids; F, forbs; DS, deciduous shrubs; ES, evergreen shrubs; DT, deciduous tree seedlings/saplings; ET, evergreen tree seedlings/saplings; M, mosses; L, lichens. Each species is also associated with a year: 1980s, indicator species for the 1980s measurement date; 2000s, indicator species for the 2000s measurement date; both, indicator species for both the 1980s and 2000s measurement dates. Species in bold are species that show up in multiple successional stages at different time periods. In particular, they highlight how the FP0 sites in the 2000s have become similar to the FP1 sites in 1980s. This illustrates a successional transition from willow–silt bars to willow–alder thickets.

Fig. 7. Significant directional and consistent change in proportion of percent cover at floodplain late-successional sites (a) white spruce (*Picea glauca*) dominated FP4s and (b) black spruce (*Picea mariana*) dominated FP5s.



pected, the success of these species in the youngest sites was followed by their decline in density and percent cover over time at the older FP1 sites. *Salix alaxensis* density declined with time at the closed alder–balsam poplar (FP2) sites to near nonexistent levels, and seedlings and saplings of balsam poplar and willows were largely absent from later successional stages. The absence of new recruits suggests that the declining density at these sites is likely due to a combination of mortality and recruitment into larger size classes (Harper 1977). We conclude that the early-successional sites (FP0s and the FP1s) are different ages of the same successional trajectory.

Similarly, there were vegetation changes in mid- (FP2s and FP3s) and late-successional sites (FP4s and FP5s) that were consistent with the turning points model. For example, we observed declines in all willow species and an increase in thinleaf alder densities from the 1980s to the 2000s in the FP1 sites (Viereck et al. 1993). We also found a break in overall plant species composition between early- and mid-successional sites (FP0s, FP1s, and FP2s) and mid- and late-successional sites (FP3s, FP4s, and FP5s) that was due, almost exclusively, to the abrupt increase in moss abundance and richness at the older sites (Turetsky et al. 2010). Finally, there was evidence that understory species composition in

the FP3s may be gradually becoming more similar to that in the FP4s, with an increase in structural and functional complexity across the chronosequence.

Observed deviations from and variation within the turning points model

We observed many vegetation patterns not predicted by the turning points model across all stages of succession. In particular, we observed shifts in species densities at early-successional sites (FP0s and FP1s), extreme variability in species composition at midsuccessional sites (FP2s and FP3s), no evidence of predicted shifts in species composition in late-successional sites (FP4s and FP5s), and landscape-level recruitment and mortality events of keystone species across all stages of succession.

Although willow abundances at early-successional sites increased, current willow densities are still much lower than in the past, resulting in unique indicator species of the FP0 sites in the 2000s that were not indicative of the FP1 sites in the 1980s (*Calamagrostis* sp., *Castilleja caudata* (Pennell) Rebr., *Hedysarum boreale* Nutt., and *Hordeum jubatum* L.). Such changes have significant implications for ecosystem function, given the large differences among these species in palatability to mammalian herbivores (Bryant and Chapin 1986) and the stabilizing effects of vegetative cover on silt bar development (Yarie et al. 1998).

Our data indicate that midsuccessional vegetation stages may be quite variable in species composition, particularly at the closed alder–balsam poplar sites (FP2) across sampling years. The lack of indicator species for these alder–balsam poplar sites (FP2s) and the older balsam poplar–white spruce sites (FP3s) suggests that species abundances rather than species presence per se may be driving the differences in these two successional stages. If species density is driving these differences, then the widespread disease-related alder mortality that has been recently documented (Nossov 2008; Ruess et al. 2009) may drastically change future trajectories for these midsuccessional stands. The cause of this variation is likely due to beaver herbivory on balsam poplar at one of the FP2 sites that began in the 1990s and is continuing into the 2000s. Although we have only quantified the consequences of beavers on midsuccessional stands at this site, beaver numbers have increased substantially over the past 15 years and their small-scale logging of balsam poplar stands is now a fairly common feature of the floodplain (personal observation). Localized variation in the intensity of animal disturbance may cause similarly aged sites to diverge, at least temporarily, in successional trajectory.

Our data also indicate deviations from the turning points model at mid- and late-successional sites (FP3s, FP4s, and FP5s). Deviations were particularly striking for seedlings and saplings of black spruce and the late-successional shrub *A. viridis*. Had the FP4 sites represented a turning point between white and black spruce dominance, we would expect recruitment of black spruce seedlings and saplings to begin at those sites, in conjunction with the slow development of permafrost. Black spruce failed to recruit at these sites, and after 25 years, there is no evidence of permafrost at these sites (www.lter.uaf.edu/data_detail.cfm?datafile_pkey=3). In addition, the species composition of the white spruce sites (FP4s) showed no indication of becoming more similar in

species composition to the black spruce sites (FP5s). Our community composition analysis (via ordination and indicator species analysis) suggests, in contrast, that these sites were fairly stable in species composition. This stability could indicate that the FP4 and FP5 sites do not represent successive stages of succession, or it could simply arise because the transition time between those stages may be quite long.

Across all successional stages, two keystone species, white spruce and thinleaf alder, showed striking patterns not predicted by the turning points model. Density of white spruce at the FP2 sites was much lower than expected and seems unlikely to achieve the densities observed at FP3. At the same time, over the 25 years, white spruce density has declined at the FP4 sites. Although such a decline would be expected if white spruce were being replaced by black spruce, as mentioned above, there is no indication that those sites are succeeding to black spruce dominance. Each of the three stages at which white spruce is present thus might represent its own unique trajectory, suggesting the possibility of multiple successional pathways that deviate from our chronosequence (Fastie 1995; Johnstone et al. 2010). These multiple pathways may be due to underlying differences in geomorphology, community-scale, or landscape-scale processes not originally accounted for by the turning points model or may result from conditions that differ from the past (Mann et al. 1995; Foster et al. 1998).

Because thinleaf alder plays such a prominent role in the N economy of floodplain forests (Uliassi and Ruess 2002), the timing of large landscape-scale recruitment or mortality events affecting the population dynamics of this species is likely to exert significant control over the rate and direction of succession (Ruess et al. 2009). The abrupt increase in thinleaf alder density during the early 1990s was part of a widespread increase in alder abundance across the floodplain, not only at young sites (FP0 and FP1) but also at older sites (FP2, FP3, and FP4). At these older sites, we expected that thinleaf alder densities would decline due to shading, short longevity, and inability of recruitment to keep pace with mortality (Walker et al. 1986; Viereck et al. 1993). The synchronous expansion of alder across the floodplain may be explained by a number of interacting factors and suggests that a large-scale alder recruitment (or establishment) event occurred in the 1990s, which is consistent with a recent landscape-scale study showing a striking pulse in alder recruitment in the early 1990s across diverse alder stand types along a large stretch of the Tanana River (Nossov 2008).

Potential drivers and mechanisms for the variation in vegetation patterns along the Tanana River floodplains

It is likely that environmental factors and unexpected disturbances contributed to the success of thinleaf alder in later successional stands. The persistence of thinleaf alder at older sites is most likely a consequence of its ability to exploit relatively favorable light environments in these floodplain forests (Chapin et al. 1994). Alder reproduces vegetatively and thus persists for long time periods in condi-

tions that are unfavorable for seed production (Yarie and Van Cleve 2006). A record autumn snowfall in the 1990s damaged alder canopies throughout our study area (Sampson and Wurtz 1994) and appears to have stimulated vegetative reproduction in damaged individuals. Indirectly, snow breakage, insects, and disease have increased overstory tree mortality and increased light availability (personal observation) in late-successional sites, favoring vegetative propagation of alder (Yarie and Van Cleve 2006). The increased alder density at older sites may have had a positive effect on alder seed rain and in turn stimulated expansion of alder at younger sites. These findings are consistent with recent studies of green alder dynamics in late-successional upland forests (Mitchell and Ruess 2009). They suggest that internal, species-specific population dynamics are as important, if not more important, than state factors in controlling successional trajectories at the landscape scale along the Tanana River.

The widespread expansion of alder in the 1990s and corresponding decrease in willow and white spruce seedlings/saplings (across all successional stages) are likely attributable in part to herbivory. The increase in the alder density, an unpalatable species, occurred simultaneously with the decline in willow, a highly favored species (Bryant and Chapin 1986), and closely follows a population peak of snowshoe hares (Kielland et al. 2010) and a substantial increase in moose densities within the Tanana Flats (Boertje et al. 2007; Butler and Kielland 2008). Although willow herbivory was an important part of the turning points model (Viereck et al. 1993), that model described herbivory as a control over the rate of succession, not necessarily the trajectory. Herbivory by snowshoe hares is an important factor reducing white spruce recruitment, as hare browsing can have substantial negative impacts on established white spruce seedlings during peak population densities (Walker et al. 1986; Angell and Kielland 2009). The functional responses of herbivores to differential toxicity among potential forage species have been shown to alter vegetation trajectories (Butler et al. 2007; Feng et al. 2009). Therefore, the complex temporal dynamics of hare population cycles and white spruce masting events are likely to cause the trajectory of succession to be highly variable over space and time.

In addition to herbivory, drought stress may also be contributing to the decline in net recruitment of white spruce along the Tanana River floodplain, either directly through seedling/sapling success (Brown 2006; Nossov et al.³) or indirectly via changes in reproductive allocation by older canopy trees (Selås et al. 2002; McGuire et al. 2010). The implications of declining white spruce recruitment for succession remain unknown, but it is likely that a failure of white spruce to recruit in large numbers at the younger sites may prolong dominance by balsam poplar at those sites or as balsam poplar die, a more open, older alder community may dominate instead of white spruce (Nossov 2008). This is a Tanana River successional phase that has not been previously described by the turning points model.

Finally, we saw evidence of directional and consistent changes in understory species composition in late-succe-

³D.R. Nossov, R.W. Ruess, and T.N. Hollingsworth. Climate sensitivity of thinleaf alder on an interior Alaska floodplain. *Ecoscience*. In review.

sional sites that may be unrelated to successional changes. We might expect some fingerprint of climate or other prevailing regional-scale change to manifest as a change in a particular functional group across sites that would not be expected to change in similar directions based on successional processes alone. Both white spruce and black spruce sites showed a synchronous decline in forb cover and density of late-successional *Salix* spp. In northern Alaska, forbs and deciduous shrubs are often sensitive to microenvironmental changes including vertical moss accumulation, moisture status, light availability (Chapin et al. 1995), snow depth, and snow accumulation (Sturm et al. 2001), which will be directly affected by changes in climate.

Our work demonstrates that some aspects of vegetation change during the last 25 years were consistent with the turning points model; however, many changes were not consistent and indicate important roles of biological, environmental, landscape, and climate controls over both the rate and the direction of succession along the Tanana River floodplain. We conclude that the chronosequence did capture early-successional dynamics; however, mid- and late-successional stands are changing either at a slower rate than expected or in a direction that was not predicted based on the turning points model. These results suggest that this putative chronosequence probably represents different stages of multiple successional trajectories, and variation in species composition/abundance cannot be explained solely by the turning points model. Finally, we found directional declines in some functional groups that may suggest an increasingly important role of climate in the vegetation patterns along the Tanana River floodplain.

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